Pin

Seasonal Fine Root Carbohydrate Relations of Plantation Loblolly Pine After Thinning

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INTRODUCTION

Loblolly pine (*Pinus taeda* L.) occurs naturally on soils that are frequently low in fertility and water availability (Allen et al., 1990; Schultz 1997). Despite these limitations, this species maintains a high level of productivity on most sites (Schultz, 1997). Knowledge of plantation loblolly pine root system growth and physiology is needed to understand how this species is adapted to soil resource limitations, and how management can be used to favor root system function.

The fine root dynamics of mature conifers is modal with a distinct

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surge of growth in spring, and the variable occurrence of a second flux of growth in fall (Gholz et al., 1986; Santantonio and Santantonio, 1987). We found that the new root growth of plantation loblolly pine peaked in May through July, and continued at a reduced rate in fall without a second surge of growth (Sword et al., 1998a, b).

We are conducting intensive research in a loblolly pine plantation to identify the physiological mechanisms that control root growth, and determine how silvicultural treatments affect these mechanisms. As a component of this research, the objectives of the present study were to simultaneously document the seasonal root growth and carbohydrate concentrations of thinned and non-thinned loblolly pine, and use these results together with canopy information to propose the sources of energy for root growth.

METHODS

This study was conducted in a 15-year-old loblolly pine plantation located on the Palustris Experimental Forest in Rapides Parish, LA. The soil is a Bearegard silt loam that is inherently low in fertility. In 1981, container-grown loblolly pine from a genetically unimproved source were planted (1.8 m $\times$ 1.8 m). In 1988, 6 - 0.06 ha plots, 13 $\times$ 13 trees each, were established. Two levels of thinning (not thinned: 2,732 trees ha^{-1}, 27.3 m^2 ha^{-1}; thinned: 721 trees ha^{-1}, 7.1 m^2 ha^{-1}) were randomly applied in three replications. In March 1995, the thinned plots (25 m^2 ha^{-1}) were re-thinned from below (not thinned: 42 m^2 ha^{-1}; thinned: 15.6 m^2 ha^{-1}).

From June 1995 to January 1996, root length (mm dm^{-2}) was quantified biweekly in five Plexiglas rhizotrons per plot of two replications that were grouped as blocks based on topography (Sword et al., 1998a). At 2- to 4-week intervals from March 1995 to January 1996, ten soil cores (6.5 cm diameter $\times$ 15 cm long), were extracted from random locations in plot peripheries. Cores were pooled and live fine roots (< 1 mm in diameter) were extracted from cores, washed, frozen, lyophilized and ground in a Wiley mill (40 mesh). Live roots were distinguished based on color, pliability, cohesion between the cortex and vascular cylinder, and the presence of meristematic root tips.

Concentrations of root starch, sucrose and glucose were determined enzymatically by the method of Jones et al. (1977) with modifications

for loblolly pine. After extraction, starch, sucrose and hexoses (glucose and fructose) were enzymatically converted to glucose. Glucose was assayed by glycolysis with the production of one unit of reduced nicotinamide adenine dinucleotide phosphate (NADPH) per unit of glucose. The NADPH was quantified spectrophotometrically by absorption at 320 nm. Carbohydrate concentrations are expressed as mg g^{-1} ash-free dry weight of fine root tissue.

In one replication, photosynthetic photon flux density (PPFD) at three randomly chosen, south-facing locations in the upper and lower one-third of the canopy were measured hourly. Values of PPFD were quantified as an average of two opposing photodiodes (Sword et al., 1998a). Branch environmental measurements were initiated in April 1995 and terminated in July due to electrical failure. Values of PPFD are expressed as the mean of four hourly midday measurements between 10:00 a.m. and 2:00 p.m.

Cumulative root lengths were transformed to natural logarithm (Y + 1) values where Y was equal to root length to insure that the data were normally distributed. Transformed root length data collected at each measurement interval were subjected to analyses of variance using a randomized complete block design with two replications. To obtain normally distributed root carbohydrate data for the evaluation of root carbohydrate concentrations in response to measurement interval, transformed data (natural logarithm [Y + 1], where Y = carbohydrate concentration), were grouped into three time periods (March-May 1995, June-August 1995, and September 1995-January 1996). Carbohydrate data in each time period were subjected to analyses of variance using a randomized complete block, split plot in time design with two replications. Main and interaction effects were considered significant at $P < 0.05$, and significantly different means were compared by the Ryan-Einot-Gabriel-Welsch multiple range test at $P < 0.05$, unless otherwise noted (SAS Institute, 1991).

RESULTS

Fine root starch and sucrose concentrations were significantly different within the three time periods (Table 1). Fine root starch concentration was greatest in March and April (98.8 mg g^{-1}), decreased significantly between April and May, continued to decrease during June through August and reached a minimum in late July and August

TABLE 1. Probabilities of a greater F-value associated with fine root starch, sucrose and glucose concentrations during March-May 1995, June-August 1995, and September 1995-January 1996 in a 15-year-old loblolly pine plantation subjected to two levels of thinning treatment.[1]

Source	df	Carbohydrate (mg g^{-1} dry weight)		
		Starch	Sucrose	Glucose
March-May 1995				
Block (R)	1	0.6992	0.2956	0.0025
Thinning (D)	1	0.4176	0.0852*[2]	0.0077*
Time (T)	4	0.0024**	0.0200**	0.0716
T × D	4	0.8937	0.4416	0.9361
June-August 1995				
Block (R)	1	0.9291	0.9265	0.3201
Thinning (D)	1	0.9163	0.3757	0.4799
Time (T)	4	0.0508*	0.0362**	0.2507
T × D	4	0.0142**	0.6464	0.4336
September 1995-January 1996				
Block (R)	1	0.8930	0.3720	0.8940
Thinning (D)	1	0.2256	0.1840	0.3870
Time (T)	3	0.0009**	0.0035**	0.0012**
T × D	3	0.6231	0.2731	0.3822

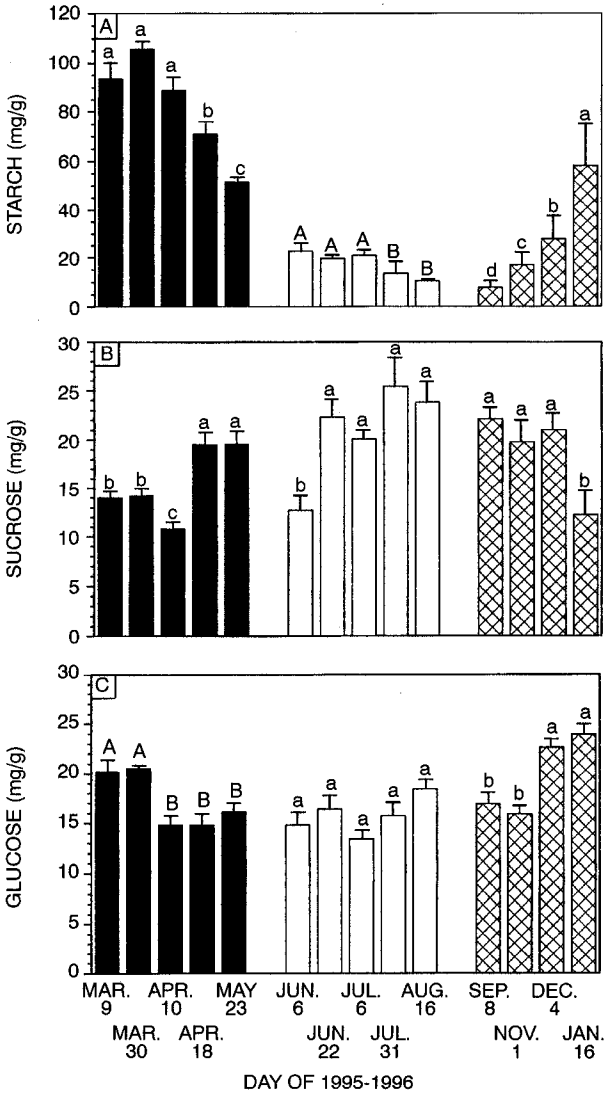
[1] Analyses were conducted on transformed data [natural logarithm (Y + 1), where Y = starch, sucrose or glucose concentration].
[2] Significance at $P < 0.05$ and 0.10 are noted by "**" and "*", respectively.

(12.0 mg g^{-1}) (Figure 1). During September-January, significant increases in fine root starch concentration were observed monthly. Significantly lower fine root sucrose concentrations were observed in March (14.1 mg g^{-1}), April (10.8 mg g^{-1}), early June (12.7 mg g^{-1}), and January (12.2 mg g^{-1}). Mean fine root sucrose concentrations in May, mid-June-August, and September-December were 19.6, 23.0, and 21.0 mg g^{-1}, respectively.

Fine root glucose concentration varied significantly in March-May ($P < 0.10$), and September-January (Table 1). Significantly greater fine root glucose concentrations were observed in March (20.4 mg g^{-1}), than in April-May (15.2 mg g^{-1}), and in December-January (23.3 mg g^{-1}), than in September-November (16.4 mg g^{-1}) (Figure 1).

The concentration of sucrose in fine roots was significantly in-

FIGURE 1. Fine root starch (A) sucrose (B) and glucose (C) concentrations of 15-year-old loblolly pine during three time periods: March-May 1995 (black bars), June-August 1995 (white bars), and September 1995-January 1996 (hatched bars). Within time periods, means associated with the same letter are not significantly different by the Ryan-Einot-Gabriel-Welsch multiple range test at $P < 0.05$ (lower case) and $P < 0.10$ (upper case). Error bars represent one standard error of the mean.



creased (21%) in response to thinning during March-May ($P < 0.10$), but was unaffected by thinning during June-August, and September-January (Table 1). Similarly, thinning was associated with a small but significant increase (2%) in fine root glucose concentration during March-May.

At each measurement interval except July 25 and August 8, the cumulative root length in rhizotrons was significantly greater on the thinned plots than on the non-thinned plots at $P < 0.05$ (Figure 2). On July 25 and August 8, cumulative root length was significantly increased in response to thinning at $P < 0.10$.

Mean midday bidirectional PPFD in the lower crown of the thinned plot (205 $\mu mol\ m^{-2}\ sec^{-1}$) was 40% greater than that on the non-thinned plot (147 $\mu mol\ m^{-2}\ sec^{-1}$). In the upper crown, bidirectional PPFD was 11% greater on the thinned plot (813 $\mu mol\ m^{-2}\ sec^{-1}$) than on the non-thinned plot (733 $\mu mol\ m^{-2}\ sec^{-1}$).

DISCUSSION

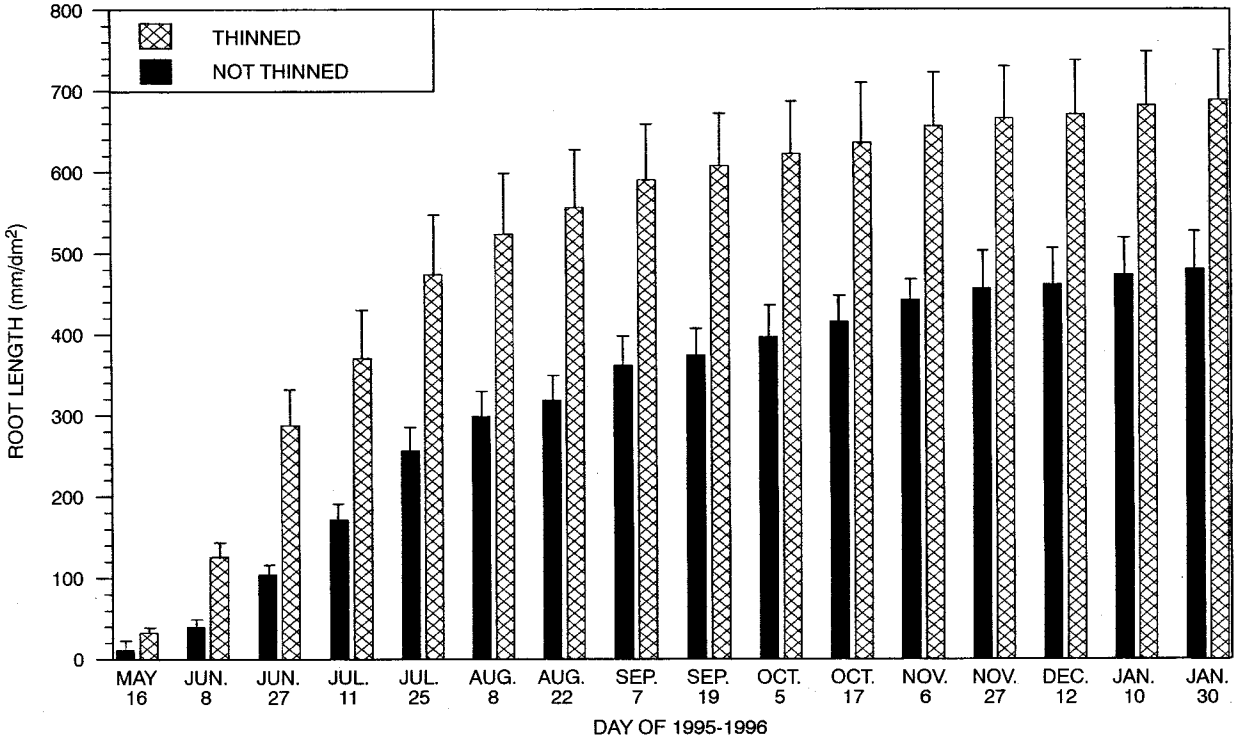
Fine root starch and glucose concentrations of loblolly pine exhibited distinct seasonal patterns. Starch concentration was greatest in March through early April, declined to a minimum in late July and August, and began accumulating in November. This pattern of root starch dynamics is similar to those reported by other investigators for southern pine species in forest stands (Adams et al., 1986; Gholz and Cropper, 1991).

The concentration of glucose in fine roots decreased between late March and mid-April, remained relatively constant between mid-April and early November, and increased in early December. This pattern may delineate the period of maximum loblolly pine root metabolism. At our study site, therefore, rhizotron measurements of loblolly pine root phenology and growth must start in March rather than May.

We have observed that the majority of loblolly pine root growth occurs in late spring and summer (Sword et al., 1998a, b). In the present study, root growth in May through June corresponded to the period of starch depletion from fine roots. This suggests that stored starch is one source of energy for spring root growth.

Fine roots consistently contained sucrose during the period of starch depletion indicating that a carbohydrate source, in addition to starch, was available for root metabolism in spring. During spring and

FIGURE 2. Cumulative length of 15-year-old loblolly pine roots in rhizotrons on thinned and non-thinned plots during May 1995-January 1996. Within all measurement intervals except July 25 and August 8, means were significantly different at $P < 0.05$. Means associated with July 25 and August 8 were significantly different at $P < 0.10$. Error bars represent one standard error of the mean.



summer, the crown of loblolly pine grows vigorously with the formation of two to four successive flushes (Stenberg et al., 1994). In general, photosynthate is preferentially allocated to developing branches until new foliage becomes autonomous at approximately 50% expansion (Dickson, 1989; Dickson, 1991). In our study, the fascicles of the first flush reached 50% expansion in mid-June (Tang, personal communication). Before mid-June, therefore, it is unlikely that root growth was sustained by the age class of pre-existing fascicles that functioned as an energy source for new shoot growth.

Gordon and Larson (1970) used $^{14}CO_2$ to determine the pattern of photosynthate allocation after assimilation by one- and two-year-old needles of four-year-old red pine (*Pinus resinosa* Ait.). They found that photosynthate produced by the one-year-old needles was predominantly allocated to shoot growth, and that produced by the two-year-old needles was allocated to root growth. We hypothesize that before mid-June, sucrose produced by the foliage of the youngest pre-existing flush was allocated to new shoot growth, whereas that produced by older pre-existing foliage was allocated to root growth.

In addition to photosynthate produced by older foliage, stored carbohydrates may have been mobilized in the stem and older foliage, translocated to the root system and used as an energy source for root growth in spring (Egger et al., 1996;, Hansen et al., 1996; Schier, 1970). After labeling red pine seedlings with $^{14}CO_2$, Schier (1970) found that mobilized ^{14}C in the roots originated primarily from two-year-old needles. Egger et al. (1996) found that high concentrations of starch and sugar were stored in the pre-existing needles, sapwood and bark of Norway spruce (*Picea abies* [L.] Karst.) seedlings in winter and spring, and suggested that a portion of these reserves was mobilized for root growth.

Fine root sucrose concentration was variable during the growing season. The increase in fine root sucrose concentration observed between April and May may have been caused by a positive effect of spring warming on photosynthesis (Teskey et al., 1994). In mid-June, the concentration of sucrose in fine roots increased and remained elevated until January. This increase in fine root sucrose concentration may signify a shift in the allocation of photosynthate produced by the youngest flush of the previous year. Specifically, autonomy of the newly developed fascicles in mid-June may have resulted in basipetal allocation of photosynthate produced by the youngest flush of the

previous year and a mid-June increase in the availability of sucrose for root metabolism.

On forest sites with limited mineral nutrient and water resources, silvicultural manipulation of root carbohydrate availability could be valuable if, in turn, new root growth increased. In our study, new root growth was stimulated by thinning. We did not observe an effect of thinning on fine root starch concentration suggesting that thinning did not influence the role of root starch in early root growth. Thinning, however, was associated with an increase in fine root sucrose and glucose concentrations in March through May. Elevated concentrations of fine root sucrose and glucose on the thinned plots during this period may be attributed to an increase in the allocation of photosynthate from older foliage, or greater mobilization of stored carbohydrates from the older foliage and/or stem.

Similar to Gravatt et al. (1997), we observed an increase in the availability of light in the lower crown in response to thinning. In 1995, Yu (1996) found that the leaf area per tree on the thinned plots was greater than that on the non-thinned plots. As older foliage became shaded, its carbon balance may have decreased below the light compensation point resulting in senescence (Schoettle and Fahey, 1994). Perhaps the positive effect of thinning on loblolly pine root growth was caused by several factors. First, thinning increased light availability in the lower crown and leaf area per tree. As a result, the basipetal translocation of photosynthate or mobilized carbohydrates from the older fascicles and/or stem during spring was increased and early root growth was stimulated. Maintenance of a nearly constant difference in cumulative root length between thinned and non-thinned plots after late June, and the absence of additional significant effects of thinning on root carbohydrate concentrations after May, suggest that the positive effect of thinning on root growth occurred early in the growing season and persisted through January.

CONCLUSIONS

Seasonal patterns of root growth and carbohydrate dynamics in our study suggest that both root starch and translocated sucrose were sources of energy for loblolly pine root growth. Thinning resulted in a greater concentration of sucrose in fine roots during spring, and more cumulative root length throughout the growing season. The positive

effect of thinning on loblolly pine root sucrose concentration and growth may have been governed by increases in light availability and the leaf area of pre-existing foliage. Further research is warranted to investigate the influence of different age classes of foliage on loblolly pine root growth, the effect of the stand environment on fascicle abscision, and the effect of premature foliage loss on root growth.

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